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THE STRUCTURE OF THE UREDINIUM IN PUCCINIASTRUM AGRIMONIAE

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A number of genera of the Melampsoraceae (Uredinaceae) are characterized in the uredinial stage by definite, punctate, usually small sori. Each sorus is surrounded by a peridium composed of cells which are more or less isodiametric when seen in face view and which form a membrane-like tissue. The genera *Pucciniastrum*, *Melampsoridium*, and *Melampsorella*, belonging to the subfamily Pucciniastratae, have uredinia of this type. Although the peridium is quite fragile in appearance, it is nevertheless true that the sorus maintains its shape remarkably well; and the spores make their escape only by a central pore until the sorus is quite aged. The spores, whether borne in chains or on pedicels, are easily loosened from their attachment and so, quite early in the development of the sorus, lose their original arrangement and become packed in without any special order.

The customary method of studying rust morphology with dried herbarium material (*i. e.*, by scraping up the spores or by cutting free-hand sections) is not sufficient, in the case of many sori of this sort, to give results of reasonable certainty. Especially is this true when an attempt is made to learn the manner in which the spores are borne, although such technique is amply satisfactory for the study of coarser details in many other kinds of sori. It has been only rather recently, however, that a full realization of the limitations of the value of free-hand sections in this group has come about.

The mature urediniospore (fig. 4) has an echinulate wall and usually an easily discernible hilum, both of which features are especially characteristic of pedicellate spores. When, therefore, such spores were

found without any special arrangement in the sorus the situation was not considered unusual. This condition is common with uredinia and, coupled with a marked indistinctness of the structures at the base of the sorus, led naturally to the conclusion that the spores were pedicellate and that the short pedicels were concealed in what appeared to be a mass of intertwining hyphae. Under this impression the descriptions and classification of the *Pucciniastratae* were published by Arthur¹ in the North American Flora, work previous to that time having thrown no doubt on the correctness of the view.

The first intimation that the accepted idea might be wrong came with the announcement by Liro² that the urediniospores of *Melampsorella Cerastii* (Pers.) Wint. are borne in chains. This point was developed somewhat and the sorus of *M. Cerastii* figured the next year in a paper by Magnus.³ The work of these two investigators, therefore, raised the question as to whether or not the urediniospores in the genera with similar sori were not also catenulate. It became, consequently, a matter of some importance to study these rusts in a more careful way than is possible with free-hand sections.

The writers began their work on October 3, 1913, by fixing some sori of *P. Agrimoniae* from leaves of *Agrimonia parviflora* Sol. The material was found growing near Lafayette, Indiana, and was the only fresh material of the group available. Part of it was fixed in chromoacetic acid and part in Flemming's weaker solution. It was imbedded in paraffin in the usual way and stained with the triple stain, the chief aim being to study the morphology of the sorus rather than nuclear phenomena.

From the material in hand it has been possible to make out that in *Pucciniastrum Agrimoniae* (Schw.) Tranz. the uredinium begins as a small aggregation of hyphae under the epidermis. Presently some of the hyphae become erect, thickened, and divided by cross walls into three or four cells each. The apical cells of the columns elongate considerably and the protoplasmic contents become less dense, as is shown by a tendency to stain less deeply than at first. They are evidently the first peridial cells to be differentiated and the other cells of the chains are spores. No intercalary cells were seen and no chains were observed having more than three or four spores to

¹ N. Amer. Fl. 7: 97, 105-117. 1907.

² Uredineae Fennicae Finlands Rostsvampar 490, 492. 1908.

³ Ber. Deutsch. Bot. Ges. 27: 320-327. 1909.

the chain. The peridial cells at this stage are much longer in a vertical direction than they are in the mature sorus, and their side walls, instead of being oblique, are perpendicular (fig. 1). The later change in shape is probably due to the pressure of the spores as they are produced. Such a pressure coupled with the decreasing cell turgor would tend to collapse the cells somewhat and to press their bases laterally.

Sections at a later stage show that as the sorus develops the epidermis of the host is lifted from the mesophyll; and this separation of the surface layer from the underlying tissues often extends for some distance beyond the very definite lenticular sorus. The mesophyll tissues are apparently not at all or only slightly injured. Often the cells directly under the center of a mature sorus retain their shape perfectly. Only a little mycelium can be seen under the sorus and none beside or over it; in fact the amount of vegetative mycelium visible at any stage is very small. The mature sorus (fig. 3), as may be inferred from what has just been said, is a very clearly differentiated structure which is sharply set off from the host tissue and from the vegetative mycelium. It is bounded above and at the sides by a peridium of somewhat overlapping, thin-walled cells in which the overlapping above the center is in a manner opposite to that of the shingles on a roof. At the side of the sorus, the direction of the overlapping becomes indefinite, so that from this point to the hymenial layer the cross walls may be oblique in either direction or some in one and some in another. The cells are usually so much collapsed that it is impossible to make out details accurately even in stained paraffin sections; but in spite of its fragile appearance it is evident that the peridium has considerable tensile strength, for the sorus maintains its shape and, until it is quite aged, furnishes no means of escape for the spores except a central ostiole. At this point, the peridium later begins to disintegrate. The ostiole is bordered by a ring of cells (fig. 2) which are larger and thicker walled than those of the rest of the peridium.

The base of the sorus is characterized by a plate-like hymenial layer of hyphal cells which at its margin often appears almost or quite continuous with the peridium and which separates the sorus from the underlying structures with a definiteness unusual in rust sori. The spore chains rise from a layer of basal cells just above the hyphal plate layer. In the young sori, where the chains are clearly visible,

of more nearly approximating a natural order. It has now been shown the plate-like layer is not very evident and in mature sori the chains are difficult to make out.

The spores and other cells which go to make up the uredinia, and the telia as well, are binucleate. Such a condition is naturally expected when the sporophytic stage of a pleomorphic rust is under consideration. The nuclear state of the free hyphae could not, however, be determined; but doubtless they are also binucleate. Nothing in the nature of hyphal fusions was observed. This is not unexpected in the consideration of the uredinial habits of this species, for normally fusions occur in the aecial stage; and all species of the genus *Pucciniastrum* are presumably heteroecious.

The mature urediniospores (fig. 4) of *Pucciniastrum Agrimoniae* are obovoid in shape, not angular, and, as already mentioned, have a more or less distinct hilum. The wall is distinctly echinulate. These are characters commonly associated with pedicellate spores, and when found in catenulate spores, where only short chains can be seen, must evidently be taken to indicate that the terminal spore matures and becomes detached before the next one has advanced far in its development. The spore next to the free end of the chain then develops in exactly the same manner, and so the process is repeated as long as spore production continues. The association of the catenulate habit and the echinulate condition is worthy of remark. The writers are unfamiliar with any other genus, except *Melampsorella*, in which such association has been shown, although presumptively it may also occur in the nearly related *Melampsoridium*. Catenulate spores are usually verrucose except in the case of some teliospores, in which instance they are smooth, never echinulate.

The peridium, as mentioned above, is formed in a way analogous to that in the ordinary aecidium. One wonders how it is produced in similar sori with pedicellate spores, as in the fern genera *Uredinopsis*, *Hyalopsora*, and *Milesia*, and could wish that Bartholomew's⁴ recent work with *Hyalopsora Polypodii* had cleared up the point for that species. It would perhaps not be too daring to risk the opinion that in such cases the roof cells are formed from the first urediniospores and produced in the same manner as in sori in which the spores are borne in chains.

With the data now at hand it would seem to be possible to suggest a new arrangement of the genera of the *Pucciniastratae* with some hope

⁴ Bull. Torrey Bot. Club 43: 195-199. 1916.

that the urediniospores in certain species of *Melampsorella* and *Pucciniastrum* are catenulate, although sometimes appearing much as if pedicellate; and it does not seem to be unreasonable to anticipate that the same condition is to be found in *Melampsorium*. In addition, it is now also definitely established by Bartholomew's work that the true pedicellate habit is to be found in *Hyalopsora*; and it is at least highly probable that the same condition is typical of the other fern rusts. Now, if these assumptions prove correct, there is provided a set of invariable characters upon which the larger divisions of the group may be separated. The points of distinction formerly used, such as wall color or number of cells in the teliospore, are often variable to a large degree within the same sorus.

This method of dividing up the group would give two subgroups, in one of which the urediniospores are borne singly on pedicels and in the other of which, when present, they are borne in chains with each chain maturing but one spore at a time. To the first of these two subgroups would belong the three fern rust genera *Uredinopsis*, *Milesia*, and *Hyalopsora*; while to the latter would belong the genera *Pucciniastrum* (*Thekopsora*), *Melampsorella*, *Melampsorium*, and *Calyptospora*. *Calyptospora*, a genus without uredinia, is nevertheless included because such characters as it possesses show close affinity to *Pucciniastrum*. This genus, therefore, gives no real trouble in this connection, even though it could not be taken care of in a working key if uredinal characters only were used in the division.

The division of the *Pucciniastratae* along the line suggested has the additional fact in its favor that it groups the fern rusts together and separates them from those rusts of the group which have the sporophytic stage on spermatophytes. Because of the evident similarity of the fern rusts, such a change has always been desirable, but until now lack of sufficient morphological information has prevented it.

It is possible, of course, that further study within the group will bring to light facts which will make necessary a further realignment of the genera. However, from the data now at hand it would seem that the grouping here suggested is more nearly along natural lines than any heretofore proposed.

The writers wish to acknowledge here the aid received from Dr. J. C. Arthur, Prof. H. S. Jackson, and Dr. F. D. Fromme, to whom they are indebted for a number of helpful suggestions.

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EXPLANATION OF PLATE VIII

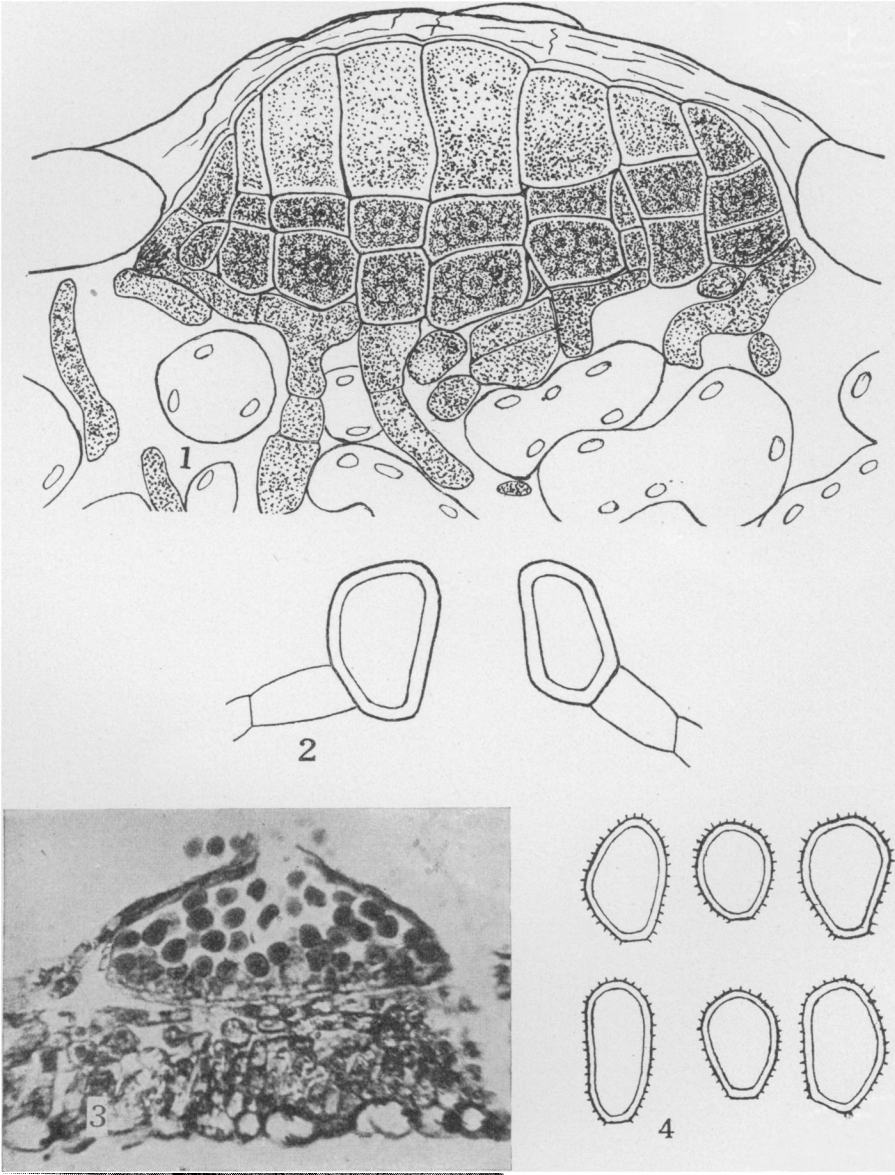
All drawings were made with the camera lucida, and all illustrations are from stained microtome sections except No. 4, which was made from spores scraped from a dry herbarium specimen and mounted in water.

FIG. 1. Young sorus of *Pucciniastrum Agrimoniae*. $\times 1360$.

FIG. 2. Vertical section of ostiole of mature sorus. $\times 1360$.

FIG. 3. Mature sorus of *Pucciniastrum Agrimoniae*. $\times 290$.

FIG. 4. Outline sketch of urediniospores. The hilum is indicated at the bottom of the spore in each case. $\times 825$.



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